

# ON THE NAUTILOID *LEUROCYCLOCERAS* FROM THE LUDLOVIAN OF WALES AND THE WELSH BORDERLAND

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ABSTRACT. Wahlenberg's species *Orthoceratites imbricatus* is discussed and considered a *nomen dubium*. The characteristic isolated cameral moulds from the upper part of the Ludlovian (Silurian) of Wales and the Welsh Borderland, which have been commonly referred to this species or to *Orthoceras marloense* Phillips, are assigned to the genus *Leurocycloceras* Foerste, under the new specific name *L. whitcliffense*. The latter species is fully described and problems of the preservation and interpretation of the moulds are discussed. It is concluded that *Leurocycloceras* provides decisive evidence for the organic origin of cameral deposits.

THE highest (Whitcliffian) stage of the Ludlovian in Wales and the Welsh Borderland (Holland, Lawson and Walmsley 1963) is characterized by a shelly fauna, new to the area, in which brachiopod species are relatively few and molluscs important. Among the latter occurs a group of distinctive, and indeed diagnostic, nautiloid cephalopods. There is a tendency for elements of the Whitcliffian fauna to appear earlier in south-easterly districts of the Welsh Borderland (Holland and Lawson 1963). Thus some of these fossils are already present in the preceding Leintwardinian Stage in the south and east, while to the north-west, e.g. in Clun Forest, the Whitcliffian itself begins with very poorly fossiliferous strata. In this latter situation the nautiloids may be conspicuous among the first traces of the Whitcliffian fauna. One of the commonest of these is the form which has been known for many years as *Orthoceras imbricatum* Wahlenberg or as *O. marloense* Phillips. Stamp (1919, p. 228) noted it as the commonest fossil in the *Rhynchonella* Beds of part of Clun Forest, and Holland (1959, pp. 453–4), in the Knighton district, Radnorshire, recorded its first appearance in strata 'in which occasional members of the fauna of the younger Ludlovian rocks begin to appear'. Both these horizons are in the lower part of the Whitcliffian. The present paper is concerned with the description of this species and the taxonomic and interpretive problems which it raises.

## TAXONOMY

The specific name *Orthoceratites imbricatus* was first used by Wahlenberg (1818, p. 89) for a nautiloid from the Isle of Gotland. His description is short and no figure was published. Foord (1888, p. 182) had already noted that no species answering to Wahlenberg's definition could be found in any of the Swedish collections and Dr. Anders Martinsson of the University of Uppsala has kindly searched again, without success, on my behalf. If a type specimen were available it might well be difficult to assign it to a meaningful genus. In its absence the species, though valid according to the International Code of Zoological Nomenclature, cannot now be interpreted and should be considered a *nomen dubium*.

Hisinger (1831, p. 112, pl. 4, fig. 4; 1837, p. 89, pl. 9, fig. 9) briefly described and [Palaeontology, Vol. 7, Part 4, 1964, pp. 525–40, pl. 83.]

figured *Orthoceratites imbricatus* Wahlenberg, again from Gotland. Blake (1882, p. 153), in reference to the 'type' of this same species, wrote: 'Wahlenberg's short description merely states that the type consists of imbricating sheaths, which are very convex, and not more than a line apart; and the siphuncle is very fine and filiform, and is central. The figure given by Hisinger ['1827' according to Blake, although this is clearly an error for 1837] to represent Wahlenberg's shell appears to have misled some, who had not referred to the latter author, to suppose the siphuncle was nearly lateral. This figure, however, may nevertheless be taken to also represent the type, especially as its inconsistencies with the description admit of explanation.' But, in further reference to Hisinger's figure, Blake notes that 'The siphuncle is too large to be called filiform, and is not quite in the centre'. Foord (1888, p. 181) took a very different view: 'The type described by Wahlenberg is stated to have an extremely slender, filiform, central siphuncle, and therefore it could not have belonged even to the same genus as Hisinger's *A. imbricatum* [Foord, following Eichwald (1860, p. 1253), refers the species to the genus *Actinoceras*], much less to that species.' There is no doubt that the latter view is the correct one as Hisinger's figure shows a relatively large siphuncle which is actually marginal in position.

Barrande (1870, pl. 440, figs. 1, 2; 1874, p. 705) resolved this difficulty by renaming Hisinger's species *Orthoceras pseudo-imbricatum*. This is fully described and illustrated and this specific name also appears to be valid. Barrande (1870, pl. 440, figs. 3, 4; 1874, p. 701) also described and figured a specimen of *O. imbricatum* Wahlenberg. The figures show a slowly expanding shell of almost circular cross-section, in which there is a small sub-central siphuncle and no trace of markings on the septal surface. The specimen is said to come from Gotland and to have had Angelin's approval, but that Barrande had reservations about its representing Wahlenberg's species is shown by his title *O. imbricatum*? Wahlenberg in the text.

However, Foord (1888, p. 182) quotes a letter received in June 1887 from Lindstrom as follows: '. . . I have had the type specimen of Barrande's *O. imbricatum* as a loan from Prague, and it is as faithfully figured in his grand work as all his specimens prove to be. I have, however, strangely enough, not found a single Gothland Orthoceratite which I may pronounce as identical with that type. I see no other way but to drop *O. imbricatum*, Wahlenberg, and keep *O. imbricatum*, Hisinger, for that long so-named, as I have proposed long ago. . . .' Foord now accepted this course, unwisely as we have seen, because *O. imbricatum* Wahlenberg, though it cannot be interpreted, is nevertheless a valid species. Barrande's solution to the problem of Hisinger's species, though not to Foord's liking, is evidently the more correct one. It is accepted as such by Teichert (1934, p. 391), who gives a full synonymy and discussion under *Armenoceras pseudo-imbricatum* (Barrande).

Blake (1882), in his monograph of British Silurian cephalopods, described and illustrated material referred to *O. imbricatum* Wahlenberg. He noted (p. 153) that 'The British specimens that are fairly referable to this species show considerable variation in many points'. As he regarded *O. imbricatum* Wahlenberg as adequately represented by Hisinger's species this is scarcely surprising. His material included those 'separate septal surfaces' with which this present paper is expressly concerned and which he found to occur 'only in the upper Ludlow, or in rocks of undefined Upper Silurian age'. It is clear that these do not belong to Hisinger's species (they do not have the wide marginal siphuncle of the latter) and they are here described under a new specific name. For-

tunately they are closely comparable with North American material of the genus *Leurocycloceras* Foerste.

Finally mention must be made of *Orthoceras marloense* Phillips. This was originally described (Phillips 1848, p. 353, pl. 13, fig. 1) as resembling *O. imbricatum* and neither Blake nor Foord could see justification for its establishment. It is certainly different from Hisinger's species as its siphuncle is approximately central. It is a valid species of which the type specimen has been examined, and I am satisfied that it cannot be made to include the 'separate septal surfaces' and other material described under *O. imbricatum* Wahlenberg by Blake. It is not well preserved, but its siphuncle appears to be relatively large as well as more centrally situated. Above all it shows no traces of the curious surface structures to be described later.

### SYSTEMATIC DESCRIPTION

Order MICHELINOCERATIDA Flower  
Family MICHELINOCERATIDAE Flower  
Genus *LEUROCYCLOCERAS* Foerste 1928

*Leurocycloceras whitcliffense* sp. nov.

Plate 83, figs. 1-10

1882 *Orthoceras imbricatum* Wahlenberg; Blake, pp. 153-5 (*pars*), pl. 14, figs. ?3, 3a, 4, 4a, 5, 6 (*non* fig. 1).

1888 *Orthoceras marloense* Phillips; Foord, p. 19 (*pars*).

1919 *Orthoceras marloense*? Phillips; Stamp, pp. 228, 244.

1963 *Michelinoceras imbricatum* (Wahlenberg); Holland, Lawson and Walmsley, pl. 7, fig. 2.

*Material.* Sixty-seven specimens, of which about one-fifth were originally collected by the author. Of the total, thirty-two specimens are in the collections of the British Museum (Nat. Hist.); ten in those of the Geological Survey and Museum; and ten in those of the University Museum, Oxford. The appropriate prefixes BMNH (British Museum) and GSM (Geological Survey and Museum) are used in the following description.

The *holotype*, BMNH C70588 (Pl. 83, figs. 1, 5), was in the Ludlow Museum Collection purchased by the British Museum in 1947 and has the label 'Silurian (Upper Ludlow) locality unrecorded (? Ludlow, Shropshire)'. The small amount of the matrix attached to the fossil is certainly typical of the siltstones of the shelf facies of the Ludlovian in the Welsh Borderland. The other eight figured specimens are BMNH C2922, C71853-7; and GSM 102290-1.

*Dimensions of holotype* (see text-fig. 1):

Length (l)	28.0 mm.
Length within rim (l')	26.1 mm.
Breadth (b)	25.0 mm.
Breadth within rim (b')	22.1 mm.
Siphuncle to ventral periphery (v)	10.5 mm.
Diameter of siphuncle (s)	4.1 mm.
Height (h)	7.0 mm.
Height above rim (h')	4.0 mm.

*Diagnosis.* Species with cross-section, position of siphuncle, and internal structures as of *Leurocycloceras*. Cameral deposits developed so strongly that internal cavity is very small, of moderate convexity, and surrounded by well-developed, steeply inclined,



pseudoseptum. Surface of hyposeptal deposits with variable system of somewhat irregular, radiating, narrow markings, arranged with some bilateral symmetry about the dorso-ventral axis. Between these are fine markings dividing peripherally. Episeptal surface with more irregular system of radiating markings dividing peripherally, and without such clear distinction of main branches and finer ones between.

*Description.* The material consists entirely of isolated internal moulds of camerae similar to those described by Flower (1941) in *Leurocycloceras* cf. *niagarensis*. The latter are dolomitized but the specimens described here are preserved in typical Ludlovian siltstone. The external proportions of the original shell are thus not known, though its cross-section was certainly elliptical, with a relatively small siphuncle placed excentrically upon its longer axis. It is reasonable to assume that the septa were concave adorally and it is likely that the siphuncle lay at the point of greatest concavity. No specimen has been traced in which the moulds are associated together in the manner suggested by Blake's description and by one of his illustrations (1882, p. 153, pl. 14, fig. 3). The cameral moulds display remarkable surface features very similar to those described by Flower (1941). There are several different modes of preservation, as follows:

(a) The surface features are best seen in the relatively common convex moulds, such as the holotype, of the kind illustrated in text-fig. 1 (and see Pl. 83, figs. 1, 2, 5). The position of the siphuncle is represented by a variously preserved, but usually slightly crater-like, structure, in which an approximately circular central area of uneven surface is limited by a rounded wall rising steeply from its external surround. Occasionally, as in the holotype (Pl. 83, fig. 1), this wall is seen to be crossed by a very faint radial system of ridges. The shorter length of the longitudinal axis of the elliptical mould, between the siphuncle and the 'rim', is occupied by an acutely triangular, relatively smooth area. This is slightly elevated in relation to the areas to the sides of it. It represents the so-called 'ventral process' (Flower 1941, &c.). The remainder of the convex surface, within the 'rim', has a pattern of radiating grooves somewhat symmetrical about the long axis. The basic arrangement of these is of a dorsal groove and three lateral grooves

#### EXPLANATION OF PLATE 83

*Leurocycloceras whitcliffense* sp. nov. All specimens are cameral moulds whitened with ammonium chloride.

Figs. 1, 5. Holotype, BMNH C70588. 'Upper Ludlow.' ? locality Ludlow, Shropshire. 1, adapical aspect ( $\times 2$ ). 5, adapical-lateral aspect ( $\times 2$ ).

Fig. 2. GSM 102290. Whitcliffian. Garth Hill, Knighton, Radnorshire. Adapical aspect ( $\times 2$ ).

Fig. 3. BMNH C2922. 'Upper Ludlow.' Ludlow, Shropshire. Adapical aspect ( $\times 2$ ).

Fig. 4. BMNH C71853. *Dalmanella lunata* Beds (Whitcliffian). Small stream south-west of Castle Bryn Amlwg, 190 yards above junction with Rhuddwr Brook, Shropshire (SO 166845). Adapical aspect ( $\times 2$ ).

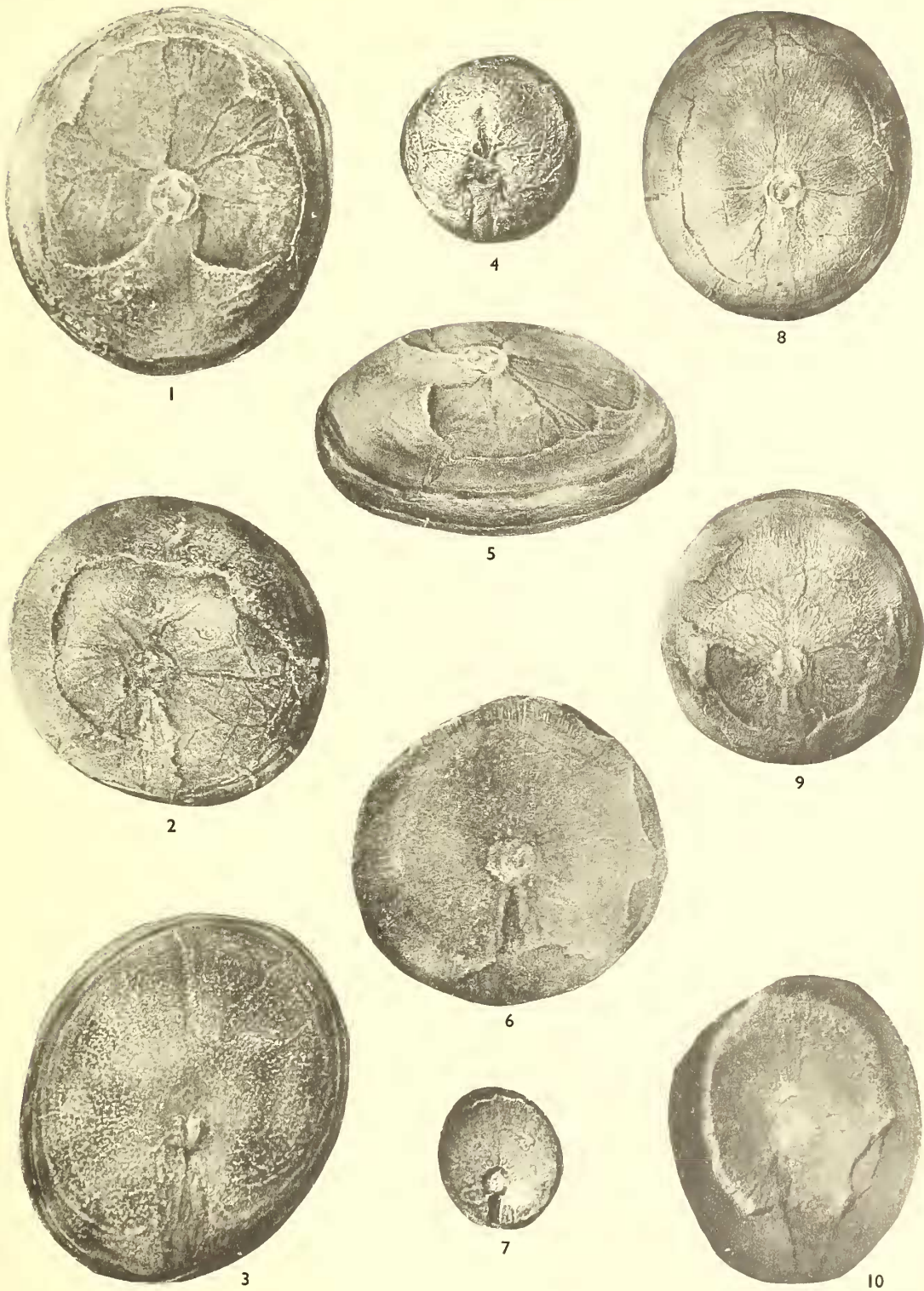
Fig. 6. BMNH C71854. Upper Whitcliffe Beds (Whitcliffian). Sunken quarry, south side Ludlow-Leintwardine road, Herefordshire (SO 442759). Adoral aspect ( $\times 2$ ).

Fig. 7. BMNH C71855. *Dalmanella lunata* Beds (Whitcliffian). Main Kerry-Clun road, Montgomeryshire, 156 yards south-east of milestone (Newtown  $7\frac{1}{2}$  m.). Adoral aspect ( $\times 2$ ).

Fig. 8. GSM 102291. 'Upper Ludlow.' Bishop's Castle, Shropshire. Adapical aspect ( $\times 1.5$ ).

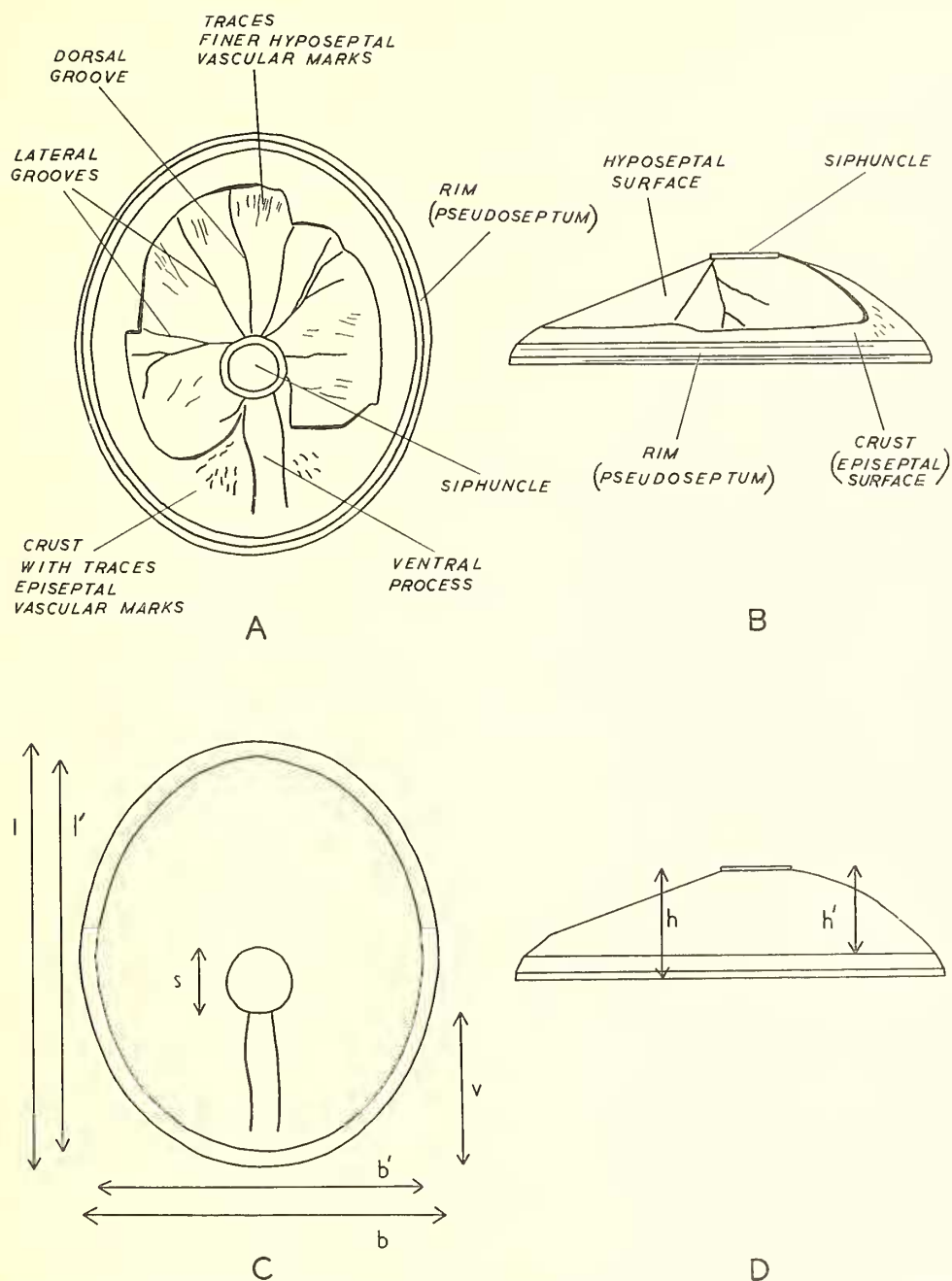
Fig. 9. BMNH C71856. 'Upper Ludlow.' Ludlow, Shropshire. Adapical aspect ( $\times 1.5$ ).

Fig. 10. BMNH C71857. Llan-wen Hill Beds (Whitcliffian). Old quarry near Warren House Farm 2 miles south-west of Knighton, Radnorshire (SO 258706). Adoral aspect ( $\times 1.5$ ).



HOLLAND, *Leurocycloceras whitcliffense*

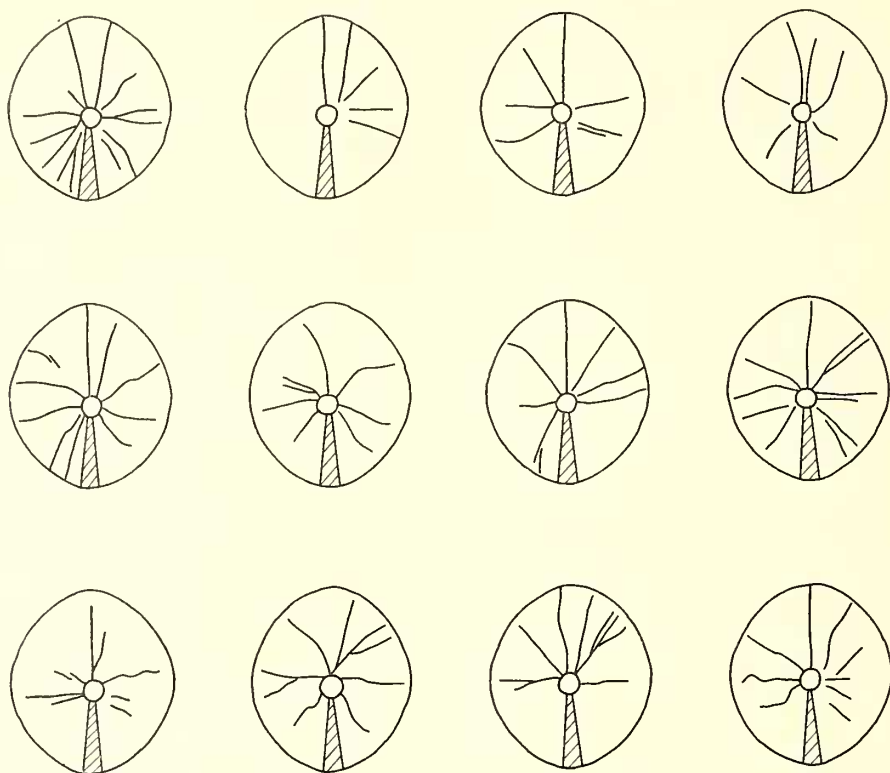




TEXT-FIG. 1. Cameral mould of *Leurocycloceras whitcliffense* sp. nov. Holotype, BMNH C70588. A, B, Simplified drawings of adapical and lateral aspects, approx.  $\times 2$ . For full details see Plate 83, figs. 1, 5. C, D, Simplified plans of A and B to show positions of measurements.



at each side. Variations are considerable, as shown by the examples in text-fig. 2; but these may be caused in part by subsequent cracking of the surface in a manner reminiscent of that seen in septarian nodules. A faint system of finer, exteriorly dividing, markings may be developed between the main radial structures as shown in text-fig. 1a and in Plate 83, figs. 1, 2, 5, 8, and 9. Frequently, as in these same illustrations, a 'crust' more or less broken from the patterned surface is present peripherally. On the surface of this crust finer markings, dividing irregularly towards the circumference, are



TEXT-FIG. 2. Simplified drawings of twelve specimens (rim omitted in each case and ventral process indicated by oblique lines) to show variation in pattern of hyposeptal grooves.

usually to be seen. The crust is a layer about 0.5 to 1 mm. thick. The convex surface with its crust is surrounded by a steeply inclined peripheral 'rim'. This rim of the mould is again variable but usually presents a series of steps and striae of the kind shown in text-fig. 1b.

The 'crust' is here interpreted as representing the sedimentary infilling of a deposit-constricted camera, and the 'rim' of the mould the position of its pseudoseptum (see Flower 1941, 1955, &c.). Thus the pattern of grooves in the central area represents an external mould of the adoral surface of this infilling and therefore an impression (twice derived) of the (adapal) surface of the hyposeptal deposit of the camera.

(b) More common, but giving an incomplete picture of the structures involved, are similarly convex moulds in which the crust is unbroken and complete, and the whole



surface within the rim covered by fine markings. The branches divide irregularly towards the periphery and may finally assume an arrangement of close parallel ridges. This second state of preservation is believed to provide moulds of the surfaces of the episepal deposits of the camerae. The ventral process is again an ill-defined acutely triangular area, which is free from vascular markings. Examples are shown in Plate 83, figs. 3, 4.

In one specimen only (Pl. 83, fig. 4) an entirely clear connexion is seen between the vascular system and the siphuncle. A similar relationship was noted by Flower in *Leurocycloceras* cf. *niagarensis* (Flower 1941, pl. 1, fig. 3).

(c) It will be apparent that specimens of the kind described under (a) above represent a condition intermediate between that of type (b) and a third type in which the whole of the crust is absent and the convex surface with its pattern of roughly symmetrical striae occupies the whole area within the rim. Specimens such as those illustrated in Plate 83, figs. 8 and 9, approach this condition, but it is very rare to find examples in which the whole of the crust is missing.

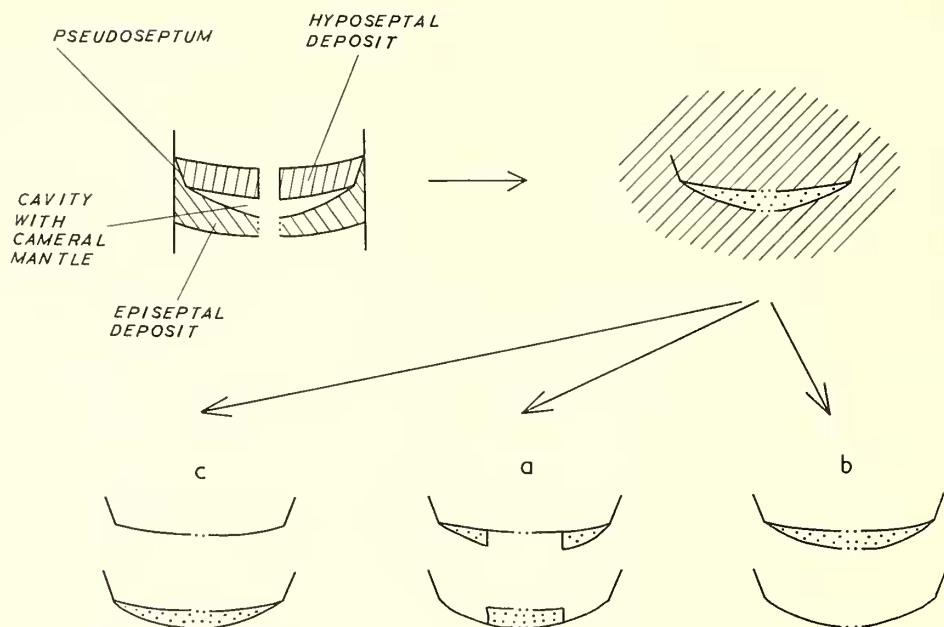
(d) In addition, it is clearly theoretically possible to find counterparts of all three types of moulds described above. Of these, counterparts corresponding to type (a) are fairly common and a few corresponding to type (b) have been examined. The former are concave moulds as in Plate 83, figs. 6, 7, and 10, in which the periphery of the concave hollow (see outer part of fig. 10) represents the finely vascular surface of type (b) and the crust (cameral infilling) itself is present towards the centre. The relative instability, once exposed, of moulds of the kind shown in Plate 83, fig. 10, especially around the periphery, probably accounts for the apparent absence of counterparts of the third type in which the crust would cover the peripheral area out to the rim. The stronger branches of the roughly symmetrical system (which in this case are preserved as ridges rather than grooves) do not show up clearly in specimens of this kind, though some may be picked out in Plate 83, fig. 10. The worn or weathered-back margin of the crust, as in Plate 83, fig. 6, may show the outer concentration of fine parallel ridges very clearly. The ventral process may appear as a break in the crust. One small specimen (Pl. 83, fig. 7) faintly reveals a system of radial tubes leading from the siphuncle into the vascular system. Like the one example of type (b) (Pl. 83, fig. 4) which shows a similar detail it is preserved in a dark brown rottenstone.

The supposed relationships of these various moulds and their modes of preservation are summarized in text-fig. 3.

The size and eccentricity of the specimens vary considerably. The data for the whole set of measurable specimens are given in text-figs. 4 (length and breadth) and 5 (position of siphuncle). Moulds of these kinds are liable to distortion in both axial and lateral senses. This may be obvious in such cases as that shown in Plate 83, fig. 2, and other likely cases appear in the graphs.

*Discussion.* Flower (1941, p. 471) confines the genus *Leurocycloceras* to species of Middle Silurian age. He observes that 'The slender form of the conch, the tendency for the development of a compressed section and the eccentricity of the siphuncle coupled with a corresponding asymmetrical curvature of each septum so that the septal foramen is at the point of greatest septal depth, have been found highly useful in recognizing the genus among other associated forms, particularly when preservation is such that the

diagnostic surface features of the shell are not clearly shown'. The material described here, in spite of its preservation, is appropriate to such a description. However, in addition, 'Internal features [of *Leurocycloceras*] are typical of the group of "*Orthoceras*" *brucense* (Flower 1939, pp. 53, 56, 57), consisting of moderately developed episeptal deposits, strongly developed hyposeptal deposits and no siphonal deposits. The connecting ring is unknown, and must have been either very poorly calcified or else altogether absent. The septal necks are unusually long and straight, and in advanced stages



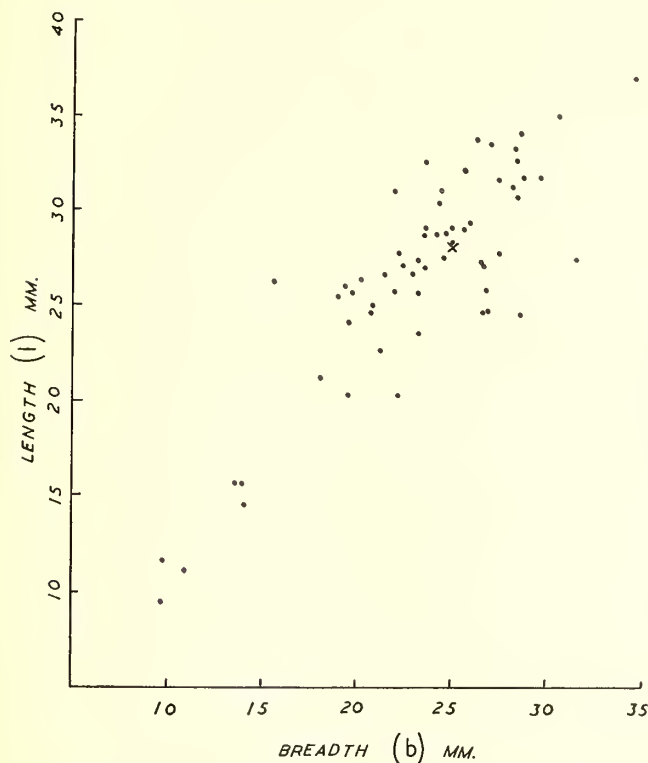
TEXT-FIG. 3. Origin and relationship of various moulds and counterparts. Top left shows one camera with internal cavity much constricted by strongly developed hyposeptal and episeptal deposits. Top right shows isolated cameral mould in matrix, derived by penetration of silt into cavity and subsequent solution of calcareous shell and cameral deposits. Lower diagrams show the three possible types of cameral mould (a), (b), and (c), referred to in the text, and their corresponding counterparts.

of growth may be entirely enclosed by cameral deposits which join through the septal foramen.' As shown in text-fig. 3, such an accentuation of the deposits will produce a long and steeply inclined pseudoseptum of the kind seen in *Leurocycloceras whitcliffense*. Such a pseudoseptum is clearly shown in the adapical camerae in Flower's diagram of *O. brucense* (Flower 1939, p. 53, fig. 11). The internal cavity in the earliest camera shown here has a degree of constriction approaching that seen in *L. whitcliffense*, though the siphuncle is shown as appreciably wider in *O. brucense*. Secondly the evidence already given of tubes leading from the siphuncle to the vascular system on the surfaces of the cameral moulds suggests that the connecting ring was either absent or relatively coarsely perforate.

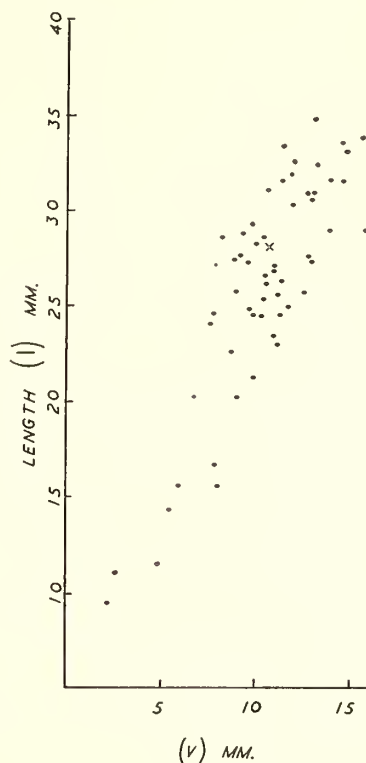
Flower (1941) further describes such features in *Leurocycloceras bucheri*. However, it is only in the dolomitized infillings of *L. cf. niagarensis* that he is able to study the surface

details of the cameral deposits. He regards some of the 'more peculiar features' as 'probably confined to the genus' (p. 483).

Amongst the North American species assigned to *Leurocycloceras* only these dolomitized cameral moulds of *L. cf. niagarens* permit close comparison with the British



TEXT-FIG. 4



TEXT-FIG. 5

TEXT-FIGS. 4, 5. 4, Length plotted against breadth for cameral moulds of *Leurocycloceras whitcliffense* from the Whitcliffian of Wales and the Welsh Borderland. 5, Length plotted against distance (v) from siphuncle to ventral periphery for almost identical set of specimens. In each figure the holotype is indicated by a cross.

material described here. *L. whitcliffense* differs from *L. cf. niagarens* in the following respects:

1. Its cameral moulds are of a different general shape, shallower than those of *L. cf. niagarens* in which a markedly convex episeptal surface is drawn out conspicuously towards the siphuncle.
2. Though certain British specimens, such as GSM 102292, illustrated by Blake (1882, pl. 14, fig. 6) and that shown in Plate 83, fig. 4 of this paper, do show a somewhat symmetrical system of relatively prominent branches on the episeptal surface, there is no such relatively regular arrangement of main radial branches of the kind seen on the hyposeptal surface. *L. cf. niagarens* has corresponding radial systems on each surface.

3. The radial tubes of *L. cf. niagarensis* are more regularly spaced and run in relatively smooth curves which bend towards the venter (as defined by the ventral process).
4. The radial structures of *L. whitcliffensis* are simple narrow grooves, whereas those of the American species show a composite structure of tube within ridge.
5. There is no trace of concentric structures on the surfaces of the British specimens, whereas those of *L. cf. niagarensis* show a prominent system of concentric ridges.

Flower (1941, pp. 473–5) discussed the possible occurrence of related species of *Leurocyloceras* in Europe. He regarded Barrande's Silurian species *Orthoceras sarcinatum* (Barrande 1874, p. 149; 1868, pl. 341, figs. 19, 20) as showing 'paired radial grooves almost identical with those shown in *Leurocyloceras cf. niagarensis*'. However, Barrande's species is based upon a single camera and was given a specific name because of its peculiar surface structure. *Leurocyloceras sarcinatum* also closely resembles the British species described here. Apart from the apparent absence of the ventral process, which may be a matter of preservation, it differs from *L. whitcliffensis* in the following respects:

1. The cameral mould is more convex than that of *L. whitcliffensis*.
2. Its radial structures are shown by paired parallel lines, indicating a composite structure closer to that of *L. cf. niagarensis* than to the simple structures of *L. whitcliffensis*.

Flower also refers 'the anomalous *Orthoceras truncatum*' Barrande (1868, pl. 341–3) to the genus *Leurocyloceras* 'with doubt'. Here Barrande suggested the occurrence of natural truncation of the shell during life—a phenomenon which requires further investigation. This form shows a complex morphology apparently involving both radial and concentric elements. Whatever its meaning it clearly has features, such as the curious shapes of some of the moulds, not to be matched in *L. whitcliffensis*.

Blake (1882, p. 155), in his description of *Orthoceras imbricatum*, notes the presence of 'similar veined septal surfaces' in *O. kendalensis*, which is said to have a siphuncle 'as nearly as possible central'. The only specimen illustrated (pl. 3, figs. 13, 13a) is from the 'Upper Ludlow' of Kendal. Its 'septal surface' shows a system of lateral markings which bifurcate once at about half or two-thirds of the distance from the siphuncle to the periphery. The type specimen of this rather slender species has been examined. Its 'septal surface' is in fact poorly preserved and the veins on it are not so clear as Blake's figure would suggest. The position of the siphuncle is eccentric, but in the opposite sense to that of *L. whitcliffensis*. No 'septal surfaces' identical with that of Blake's illustration have been found in collections from the Welsh Borderland or Wales.

*Distribution.* *Leurocyloceras whitcliffensis* occurs widely in the Whitcliffian of Central Wales and the Welsh Borderland. Its acme is in the lower part of the stage and it is commoner in western (basin facies) districts. It is particularly characteristic of those massively bedded siltstones which Holland and Lawson (1963, p. 278, and fig. 9) have separately differentiated in their facies distribution map for the lower part of the Whitcliffian Stage.

In the May Hill inlier Lawson (1956, p. 112) records it as already 'present' in the Lower Longhope Beds, which correlate with the upper part of the preceding Leint-



wardinian Stage. This is in accordance with the situation previously mentioned that elements of the Whitcliffian fauna appear earlier in the south-east.

The distribution of *L. whitcliffense* is known to include the following districts: Ludlow, Leintwardine, Onibury, Woolhope, May Hill, Usk, Bishop's Castle, Clun Forest (Kerry, south-west Clun, and Bucknell), Knighton, and Presteigne. Other published records are not necessarily reliable because of the confusion over the meaning of this species.

#### PROBLEMS OF INTERPRETATION

Nautiloid cameral deposits, supposedly secreted within the chambers of the shell by the tissues of the living animal, have been the subject of a wide and detailed literature. A selected list is given by Mutvei (1956, p. 188). Teichert (1933) differentiated between these and secondary deposits of inorganic origin and noted the importance of the organic deposits in the hydrostatic adjustment of the animal. Flower (1939) developed the concept of the 'cameral mantle' of living tissues within the chambers but connected with the siphuncle. Impressions of vascular structures on the surfaces of cameral deposits were reported (Flower 1941) from the dolomitized moulds of *Leurocycloceras* cf. *niagarensis*. Amongst many other relevant articles Flower (1955a) has provided a useful summary of the morphology, ontogeny, and significance of cameral deposits and has attempted to link this mechanism of hydrostatic adjustment of the animal to its mode of life (Flower 1955b, 1957). Both Teichert (1934) and Flower (1943) have provided evidence for the former existence of the cameral mantle, indirect in the sense that it relates to a space eventually left vacant by the decay of the soft tissues of this mantle and only subsequently filled with calcite. Flower (1939, pl. 7, fig. 8; pl. 9, fig. 19) has described a specimen in which calcareous cameral deposits are associated with calcite-filled cameral cavities, but there is a layer adjacent to the cameral deposits which is highly carbonaceous and which is thought to have been derived from the tissues of the cameral mantle.

Finally, Grégoire (1962) is already extending his observations with the electron microscope on the submicroscopic structure of the *Nautilus* shell to the examination of fossil material. He records (1962, p. 44) observations on the cameral deposits of a Pennsylvanian orthocone *Pseudorthoceras knoxense*, in which an intricate association of organic and inorganic zones is of the kind found in the sutural infillings of the *Nautilus* shell. In addition he notes probable areas of secondary inorganic material associated with the primary cameral deposits.

Mutvei (1956, p. 188), on the other hand, regards all such interpretations as erroneous and based upon an inadequate understanding of the anatomy of the modern cephalopods. He regards the cameral deposits as having been laid down secondarily by precipitation from percolating water and cites such variable lamellar structures as those found in the genus *Lamellorthoceras*.

There can be no doubt that the intricate, but relatively constant, surface markings of *Leurocycloceras whitcliffense* are vascular marks of organic origin. Their mode of connexion to the siphuncle provides additional evidence. Once this point is accepted there are two possibilities: firstly, that the vascular markings are impressions of living tissue which once lay in contact with the septal end of the living chamber of the shell;

secondly, that they record the original presence of living tissue within the completed camerae themselves.

At first sight the evidence appeared to favour the former possibility. It was already envisaged by Blake (1882, p. 154), who noted that 'These structures are probably not peculiar to the present species, since the same may be traced on the concave side of the septum of a living *Nautilus* . . .'. Referring in a more general way to these 'vascular marks' in the introduction to his monograph he makes it clear that his comparison is with the marks to be seen in the last body chamber of the modern *Nautilus*. 'They represent the impressions of circulating vessels in the upper part of the mantle, and ramify from the neighbourhood of the siphuncle, and bifurcate towards the circumference. Since each septum was at one time the end of the body-chamber, similar marks are to be found on the concave side of each, but they do not correspond to any arteries in the septal chambers, which are not in connection with the siphuncle in this way' (p. 40). Though not providing proof of a different origin, an examination of such markings on the septum of a modern *Nautilus* shell, or of the illustration by Willey (1902, pl. 82, fig. 10) of the 'paired pallial veins' which no doubt produced them, shows that the pattern of the latter, with their main branch at each side and attendant ramifications from it, is quite different from the radial system of *Leurocycloceras*.

The banded appearance of the rim of the moulds of *L. whitcliffense* at first sight invites comparison with some of the muscle impressions illustrated by Mutvei (1957) in fossil nautiloids. There are, however, several 'steps' in the rim and it shows no indication of the expanded lobes, variously but symmetrically disposed, which are a feature of the muscular 'annular elevation'.

Thus the argument leads to the conclusion that the vascular markings of *Leurocycloceras* were actually formed *within* the completed chambers as envisaged by Flower. The critical positive evidence is available if, instead of the isolated cameral moulds of *L. whitcliffense*, we turn to the dolomitized North American material of *L. cf. niagarensis*. Here (Flower 1941, pl. 1) several such moulds of successive camerae are still associated together, and markings (episeptal and hyposeptal) are seen on *both* convex and concave surfaces of the moulds. It is not difficult to imagine the shell and calcareous cameral deposits in their original positions around moulds such as those of Flower's pl. 1, fig. 1. The surface markings would then clearly be present in both adaptal and adoral positions in each chamber.

Objection to the concept of secretion within the chambers appears to be that of accepting penetration of the appropriate living tissue through the siphuncular wall. Flower (1941) explained the simple passage of branches from siphuncle to cameral mantle in *Leurocycloceras* by the absence of the connecting ring in this form. Additional evidence of the branches from the siphuncle has been provided in the present description of *L. whitcliffense*. Flower (1939) considered that in other cases the connexion might be made through 'capillary vessels' (p. 47) or by osmosis. That Palaeozoic orthoconic nautiloids may have been able to solve their considerable hydrostatic problems by such a passage of secretory tissue from siphuncle to chamber is perhaps more easily acceptable when it is realized that even in the living *Nautilus* the siphuncular wall is not an impenetrable barrier. This is becoming clearer from recent studies of buoyancy in living cephalopods. Thus the elegant experimental work at the Plymouth Laboratories on the buoyancy of the cuttlefish *Sepia* (Denton and Gilpin-Brown 1961*a, b, c*; Denton, Gilpin-Brown and

Howarth 1961) has been projected to a comparison with the living *Nautilus* (Denton 1961; Denton and Gilpin-Brown 1961a). That the siphuncle of *Nautilus* connects with the blood system of the animal has been known since the early monographs of Owen (1832) and Willey (1902), and the latter gave detailed cross-sections showing the histology of the siphuncle. The epithelium lying against the siphuncular wall of *Nautilus* has now been compared directly (Denton 1961, figs. 19, 20; Denton and Gilpin-Brown 1961a, fig. 9) with the very similar epithelium lying on the siphuncular (posterior ventral) surface of the cuttlebone of *Sepia*. The latter epithelium and wall allow the passage of liquid under osmotic control in and out of the cuttlebone, which thus serves as 'a variable buoyancy tank'. The same method thus probably accounts for the emptying of the originally liquid-filled, sealed-off chambers of the nautiloid and perhaps for its buoyancy control. Bidder (1962) has shown that recently killed *Nautilus* has a much greater volume of liquid in the newest chambers. She notes that 'The fact that the quantity of fluid changes with age in each chamber suggests that liquid can move out of, and possibly also into, the chambers; this is also consistent with the situation in *Sepia*. The control of liquid in *Sepia* is through the "siphuncular membrane", which closes the chambers; in *Nautilus* it must be through the siphuncle. . . .' 'The histology of the siphuncular epithelium closely resembles but does not appear to be exactly the same as that of *Sepia*, suggesting rather a condition from which the *Sepia* membrane could have evolved.'

In fact it seems not unreasonable to suggest that the hydrostatic control mechanism of *Nautilus* itself evolved from a still earlier stage in the Palaeozoic forms, when a 'once only' secretion of cameral deposits at appropriate positions in the shell foreshadowed the delicate fluid transfer system of the later cephalopods.

A detailed interpretation of the development of the surface impressions of *Leurocycloceras* has been given by Flower (1941). Thus, for example, the ventral process is seen as the first area of joining of the originally discrete episeptal and hyposeptal deposits. These later begin to merge from the whole periphery inwards along the pseudo-septum.

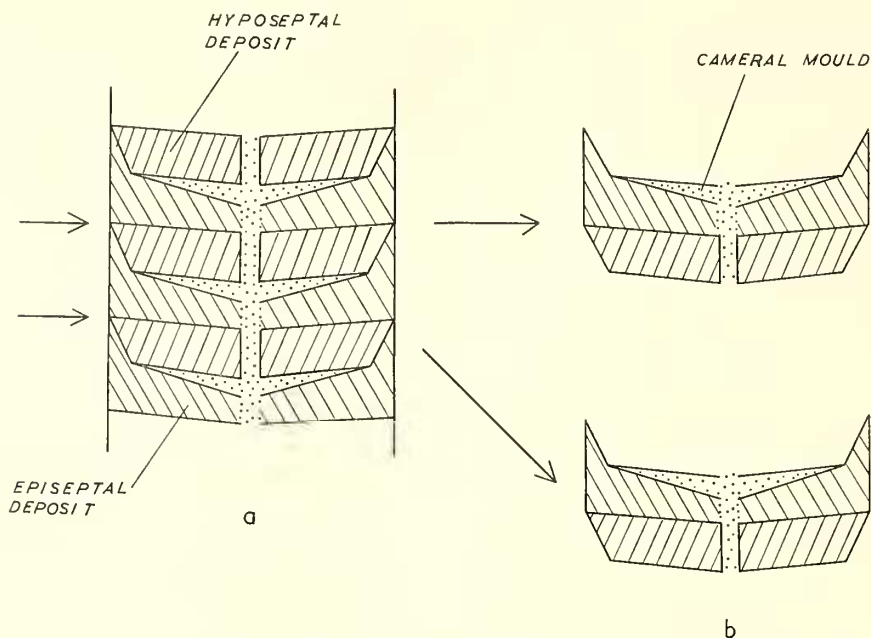
An additional difficulty of interpretation in the case of *Leurocycloceras whitcliffense* derives from the persistent occurrence of the moulds in isolation from one another.

Blake (1882, p. 35) devotes a paragraph of his introduction to the phenomenon of natural truncation of the shell as originally observed by Barrande. He regards the numerous isolated 'septa' of '*Orthoceras imbricatum*' as 'most satisfactorily accounted for if they were naturally thrown off one by one'. If this was indeed the case it would be difficult to explain the apparent absence of specimens in which two or more of the chambers (not having suffered truncation) remained together. Fortunately this difficulty is overcome when the isolated 'septa' are regarded as cameral moulds, relatively widely spaced peripherally and connected only through a mould of the siphuncle (as in Flower 1941, pl. 1, fig. 1), and therefore liable to easy separation. However, even if this is the case, it might be reasonable to expect associated groups of such separated moulds.

Flower (1955) notes that in orthoconic nautiloids with cameral deposits there are some younger (adoral) chambers in which these deposits have not formed, and that this number of chambers tends to be constant for the species. It is possible that sediment of the silty nature of the typical Whitcliffian deposits might penetrate easily into this younger part of the shell (if it existed at all) in *Leurocycloceras whitcliffense*; but that penetration back through the already filling siphuncle and restricted cavities of those



chambers in which cameral deposits had already formed was so difficult that in general only the first of the latter produced a cameral mould. Flower (1955) observed that a middle part of the shell might be expected to show immature cameral deposits, while the mature deposits occur adapically. It appears that maturity of the deposits must have been quickly achieved in *L. whitcliffense* and perhaps the final stages in the adapical camerae were such that the chambers became completely filled, to the final obliteration of the cavity. Such camerae would not produce cameral moulds and this again may account for the scarcity of the adapical moulds. The views expressed in this paragraph



TEXT-FIG. 6. A possible alternative origin of cameral moulds. *a*, Three camerae are shown with strongly developed cameral deposits and with silt infilling the cameral cavities and siphuncle. The arrows on the left indicate points of weakness of the shell. *b*, The shell is broken apart on the sea floor to produce calcareous units (two of which are illustrated) in which the cameral mould may be present in the relatively protected concavity of the adoral surface. These will be subsequently covered by sediment and the calcareous units gradually dissolved.

are supported by the fact that most cameral moulds of *L. whitcliffense* lie in a fairly restricted size group (length 23.0 to 35.0 mm.). There are very few smaller ones (cf. text-figs. 4, 5).

In summary, the isolated cameral moulds of *Leurocycloceras whitcliffense* which have been described are the result of a complex preservational history. The living form, in its maturity, is to be regarded as having had adoral chambers with the likely absence of cameral deposits, at least one middle chamber in which these deposits were strongly developed to the considerable restriction of the internal cavity, and adapical chambers which may have been completely choked with cameral deposits. After death it is postulated that silty sediment penetrated into at least the most adoral of the chambers in